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Low temperatures impact species distributions of jumping spiders across a desert elevational cline

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ABSTRACT

Temperature is known to influence many aspects of organisms and is frequently linked to geographical species distributions. Despite the importance of a broad understanding of an animal's thermal biology, few studies incorporate more than one metric of thermal biology. Here we examined an elevational assemblage of *Habronattus* jumping spiders to measure different aspects of their thermal biology including thermal limits (CT_{min}, CT_{max}), thermal preference, $\dot{V}CO_2$ as proxy for metabolic rate, locomotor behavior and warming tolerance. We used these data to test whether thermal biology helped explain how species were distributed across elevation. *Habronattus* had high CT_{max} values, which did not differ among species across the elevational gradient. The highest-elevation species had a lower CT_{min} than any other species. All species had a strong thermal preference around 37 °C. With respect to performance, one of the middle elevation species was significantly less temperature-sensitive in metabolic rate. Differences between species with respect to locomotion (jump distance) were likely driven by differences in mass, with no differences in thermal performance across elevation. We suggest that *Habronattus* distributions follow Brett's rule, a rule that predicts more geographical variation in cold tolerance than heat. Additionally, we suggest that physiological tolerances interact with biotic factors, particularly those related to courtship and mate choice to influence species distributions. *Habronattus* also had very high warming tolerance values (> 20 °C, on average). Taken together, these data suggest that *Habronattus* are resilient in the face of climate-change related shifts in temperature.

1. Introduction

A fundamental goal in biology is to explain species distributions. Temperature is one of the primary abiotic factors with predictive ability in this regard (Gaston et al., 2009; Ghalambor, Huey, Martin, Tewksbury, & Wang, 2006; Sunday et al., 2019). Environmental temperature is a particularly salient factor for ectothermic animals (those which cannot generate metabolic heat) (Angilletta, 2009; Hochachka, 2002), especially small animals whose body temperatures rapidly equilibrate with environmental temperature (Dillon, Liu, Wang, & Huey, 2012; Hochachka, 2002). Specifically, thermal tolerance (the ability to withstand extreme temperatures) is frequently measured to assess an animal's thermal biology (Angilletta, 2009).

Geographic clines in temperature shape ectotherm thermal tolerances at the inter- and intra-specific levels (Gaston et al., 2009; Sinclair et al., 2012). A number of macrophysiological "rules" have emerged from this literature. One of these, Brett's rule, predicts more geographic variation in cold, rather than heat tolerance (Gaston et al., 2009). Brett's rule has some compelling support. Species from cold habitats at high latitudes are generally found to be more cold-tolerant than those found in warm, low-latitude environments. Heat tolerance, however, tends to be more similar across latitudes and environments (Addo-Bediako et al., 2000; David et al., 2003; Kellermann et al., 2012; Kimura, 2004; Sunday et al., 2019). Among these studies, there has been strong evidence for Brett's rule in tropical populations of insects, lending support to the idea that tropical species have narrower thermal breadths and are thus more vulnerable to climate change (Janzen, 1967; Polato et al., 2018). Despite this, there have been relatively few studies looking at these principles across elevational gradients, particularly outside of tropical forest habitats (Polato et al., 2018; Sunday et al., 2019). In fact, among arthropods found across elevational gradients, support for Brett's rule has only been found in grasshoppers, ants, and aquatic insects, all in tropical systems (Arnan et al., 2014; Nowrouzi et al., 2018; Polato et al., 2018). It is crucial to increase habitat and taxonomic diversity to better understand the underlying patterns and to test the generality of macrophysiological rules (Gaston

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et al., 2009).

In addition to expanding habitat and taxonomic diversity, methodological diversity in examining thermal biology is needed. The totality of an animal's thermal biology cannot be collapsed down to only its ability to tolerate extreme temperatures. Moderate temperatures can exert selection through their effects on growth, reproduction, and other fitness characters, expressed as thermal performance curves (Angilletta, 2009; Hochachka, 2002). Shifts in thermal performance curves for these physiological or performance traits can occur in response to divergent climatic regimes and can be used to predict responses to climate change (Sinclair et al., 2016). Animals can also select favorable microhabitats that optimize performance through behavioral thermoregulation. The ability to behaviorally thermoregulate within a desired preference range can dramatically limit the subset of temperatures to which animals are exposed, and act as a buffer against thermally-stressful temperatures (Martin and Huey, 2008). Behavioral thermoregulation can thus reduce selection on both thermal limits and thermal performance curves (Muñoz et al., 2016). Despite the importance of a broad understanding of an animal's thermal biology, few studies of species distributions incorporate more than one of these metrics of thermal performance (Overgaard et al., 2014). In the following study, we measured aspects of thermal tolerance, thermal preference, and thermal performance to examine whether thermal biology explains species distributions across an elevational gradient.

Family Salticidae (jumping spiders) is the most diverse spider family (> 6000 species), and its members are ecologically important predators (Foelix, 2010; Michalko et al., 2019). Among jumping spiders, *Habronattus* is a particularly diverse genus (~110 species) found across North America. Communities of *Habronattus* species have been described in many habitats (Griswold, 1983; Richman, 1977, 1973) often spread across elevational gradients. Few studies have explored thermal biology in any arachnid, and fewer still have explicitly measured this in the context of habitat gradients (but see Mammola et al., 2019). In this study, we examined *Habronattus* species found across an elevational gradient in the Santa Rita mountain range in the Sonoran Desert. Habitats in this mountain range progress from lowland desert (hot/dry/open) to pine forest (cool/wet/shaded) with increasing elevation (DeBano, 1999). We hypothesized that aspects of thermal biology would explain the distribution of *Habronattus* species across the Santa Rita Mountains in Southeastern Arizona (hereafter referred to as SR *Habronattus*).

We first collected *Habronattus* species found at four sites along an elevational gradient in the Santa Rita Mountains (Fig. 1a–b), located in unceded lands of the Tohono O'Odham and Hohokam peoples. We then performed experiments to assess different aspects of the animals' thermal biology. We tested thermal tolerance by measuring the critical thermal limits (CT_{min} and CT_{max}) and determined whether this assemblage obeys Brett's rule. We also measured thermal performance (respiration and locomotion), and temperature preference. Finally, we compared these aspects of thermal biology to current and future environmental temperatures to predict vulnerability to climate change.

2. Materials and methods

2.1. Description of sites and species

We collected animals from four sites along an elevational gradient in the Santa Rita Mountains in SE Arizona: a low elevation (average 1201 m) desert scrub site, a middle elevation (average 1266 m) desert grassland site, a middle-high elevation (1532 m) oak woodland site, and a high elevation (1672 m) pine woodland site (Fig. 1a). We collected individuals of six *Habronattus* species: *H. virgulatus* Griswold, 1987, *H. clypeatus* (Banks, 1895), *H. conjunctus* (Banks, 1898), *H. hallani* (Richman, 1973), *H. pugillis* Griswold 1987 and *H. geronimoi* Griswold 1987. In general, each species was most associated with one elevational site although we occasionally found individuals at other sites. We only collected and performed experiments upon individuals that were found in their typical site. Specifically, *H. virgulatus* was found exclusively at the low elevation site. *H. clypeatus* was found at the middle site, but also at the low site and infrequently at the middle-high site. *H. hallani* and *H. conjunctus* were found at the middle elevation site. *H. pugillis* is known to be an oak forest specialist (Maddison and McMahon, 2000) and was found at the middle-high site. Finally, *H. geronimoi* was mostly found at the high elevation site (one individual was found in 2018 at the middle-high site).

2.2. Habitat data

We tested whether the different elevational sites were climatically and thermally distinct. We did this by recording GPS collection data for every spider collected in 2017 (sample sizes for each site: low: 82, middle: 580, middle-high: 74, high: 48). We then imported the GPS points into R v. 3.5.2, and used the WorldClim2.0 dataset (30 s resolution raster) (Fick and Hijmans, 2017) implemented using the raster package to extract Bioclim variables for those points. We used two different Bioclim variables: Maximum temperature of the warmest month, and minimum temperature of the coldest month. The first variable is thought to correspond well to CT_{max}, and the second, to CT_{min} (Kellermann et al., 2012). We also calculated a third variable, annual breadth, calculated as maximum temperature of warmest month minus minimum temperature of coldest month. We compared the climatic variables of our four different sites using an ANOVA followed by post-hoc Tukey tests.

2.3. Animal collection and maintenance

We collected spiders during March and April of 2017 and 2018. We collected animals at all life stages, but only performed experiments on individuals that had been sexually mature for at least two weeks. We used approximately equal numbers of males and females (assessed by looking for male or female genitalia) for each experiment. Animals were kept in small plastic cages and fed *Drosophila melanogaster* and pinhead *Gryllodes sigillatus* crickets once per week. We acclimated all animals to lab conditions (~24 °C) for at least two weeks before running experiments. Animals were not fed within 48 hours of any experiment. However, due to the complicated nature of our repeated-measures experimental design, we were not able to feed animals a standardized number of days prior to experiment. (Range: 2–15 days before experiment). We performed $CT_{min/max}$ trials during fall 2017, thermal performance studies during spring and summer of 2018, and preference studies during summer 2018.

2.4. Thermal tolerances

To assess thermal tolerances, we used a ramping assay that used loss of righting ability as the indicator of a limit being reached. Ramping assays have been suggested to be faster and more accurate than static assays (Kovacevic et al., 2019; Rezende et al., 2011; Terblanche et al., 2007). To perform these experiments, we used an incubator (MIR-154-PA, Panasonic Healthcare, Tokyo, Japan) and a custom device that allowed us to flip spiders throughout the ramp procedure to see at which point they lost their righting ability. See SI for more detailed methods.

For CT_{max} trials, we started the incubator at 40 °C. Spiders were acclimated to this temperature for ten minutes. We then began the trial and ramped the incubator to 60 °C. For CT_{min} trials, we used the same method, but set the incubator to 15 °C for the initial temperature and ramped to 0 °C. We flipped the spiders every 2 min and observed the spiders until they were unable to right themselves within 20 s. We measured the mass of each individual after each trial. Due to the experimental setup, we were unable to immediately remove animals from the setup after their CT_{max} had been achieved. Because of this, animals frequently died after the CT_{max} trials, so we ran CT_{min} trials first, and

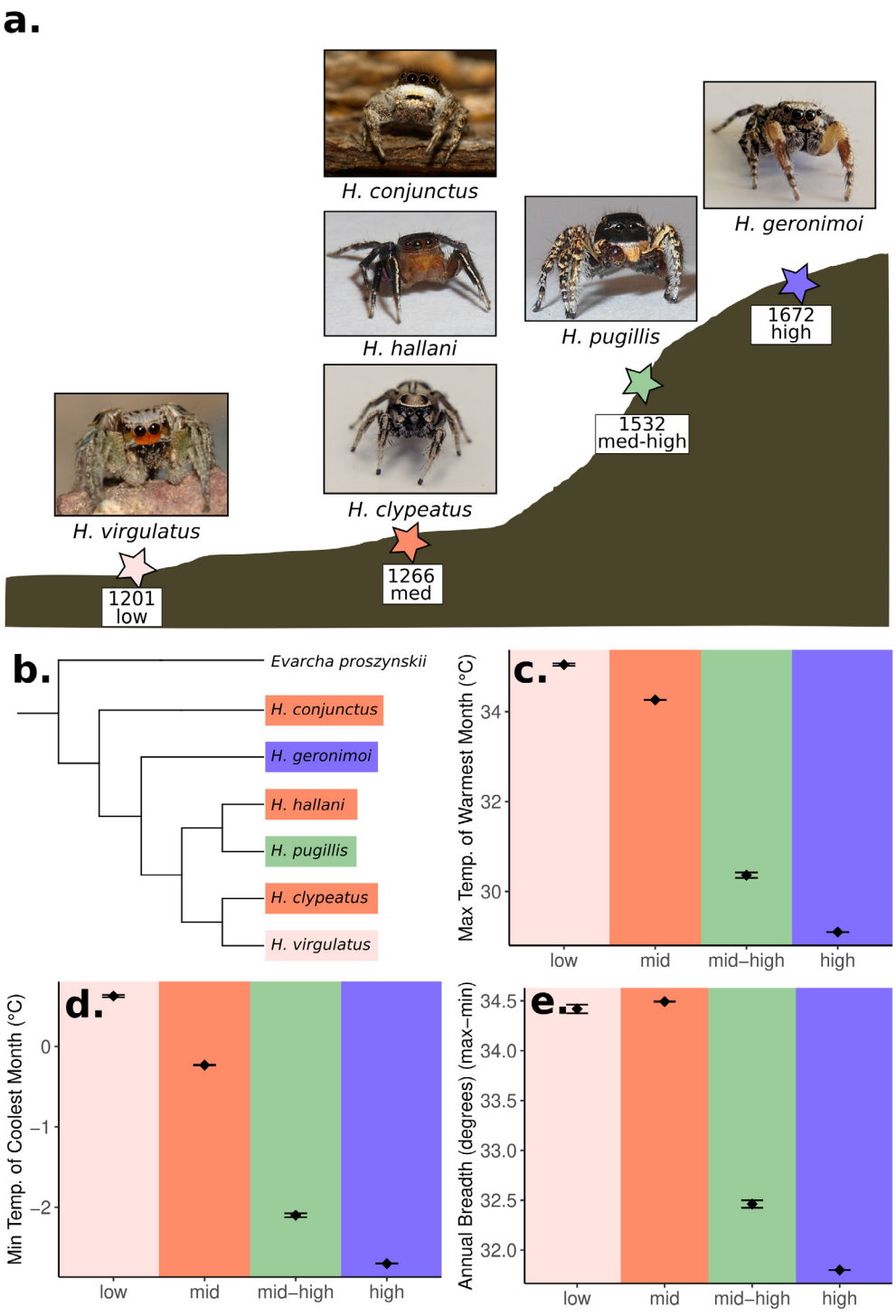

Fig. 1. Santa Rita *Habronattus* elevational distribution and environmental conditions. (a) Schematic of elevational distribution of *Habronattus* species found in the Santa Rita mountains (diagram not to scale). Collection sites are indicated with labels used throughout the paper (low, middle, middle-high, high) along with average elevation. Color coding for elevational sites is consistent across figures. All photos are of adult males. (b) Phylogeny showing relationships between the six SR *Habronattus* species. Data were taken from Leduc-Robert & Maddison, 2018. Species are highlighted with the same colors as in panel a to illustrate their elevational site. (c) Maximum temperature of warmest month for each site ± SE. All sites are significantly different from one another ($p < 0.0001$). (d) Minimum temperature of coldest month for each site ± SE. All sites are significantly different from one another ($p < 0.0001$). (e) Annual temperature breadth (minimum temperature of coldest month minus maximum temperature of warmest month) of all sites ± SE. All sites are significantly different from one another ($p < 0.0001$).

CT_{max} trials after at least 24 h of recovery time. For each trial (block), we used 4 spiders of the same species and sex. Each block thus had a slightly different ramping rate, and there were 2–5 blocks per species. To ensure that ramping rates did not differ systematically between species, potentially leading to differences in estimated thermal tolerances, we tested whether ramp rate differed with species. We found that ramp rate did not vary significantly between species for the CT_{max} trials (ANOVA: $df = 5$, $F = 2.285$, $p = 0.054$). For CT_{min} trials, ramp rate did vary between species (ANOVA: $df = 5$, $F = 9.774$, $p < 0.001$), so we included both ramp rate and block in subsequent analyses as random factors. Ramp rates for all species are shown in Table 1. To model the differences in thermal limits, we used linear models with species as the fixed factor and CT_{min} or CT_{max} as the response. No other variable (mass, days since fed, etc.) explained a significant amount of variation in critical thermal limits, aside from ramp rate and block, for CT_{min} trials.

2.5. Thermal preference

We designed a temperature gradient device to assess thermal preference, spanning a thermal gradient of about 15–60 °C. See SI for details of setup. In short, the thermal gradient was heated on one end with silicone heaters (model SRFG-110/-10P, Omega Engineering, Norwalk, CT, USA) and ceramic heat bulbs (Zoo Med Laboratories Inc, San Luis

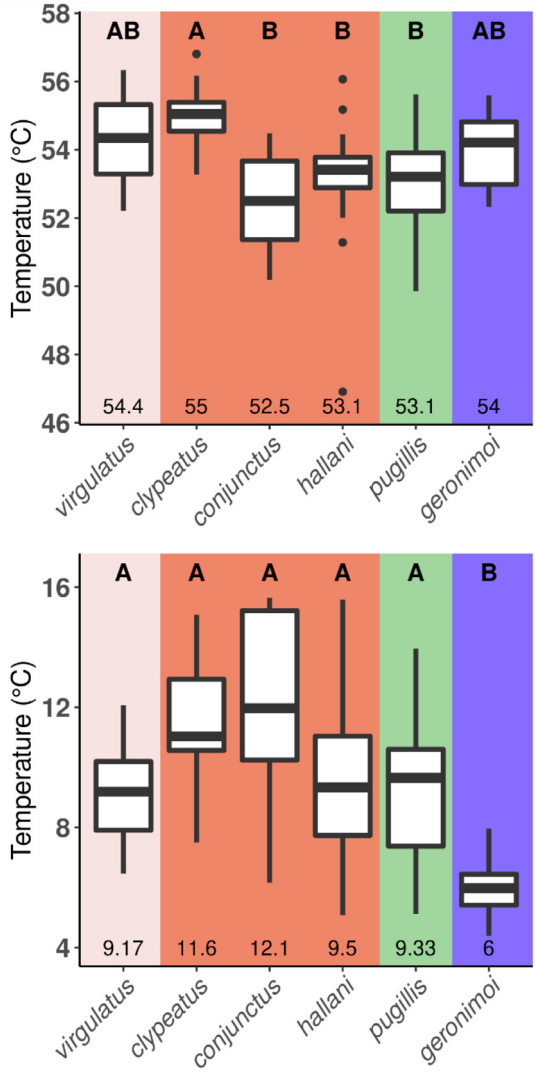

Fig. 2. Critical thermal limits in Santa Rita *Habronattus*. (a) Critical thermal maxima. Mean values are shown for each species. *H. clypeatus* is significantly different from *H. hallani*, *H. conjnctus*, and *H. pugillis*. No other differences are seen. (b) Critical thermal minima. Mean values are also shown for each species. Note that *H. geronimoi* is significantly different from all other species except for *H. virgulatus*. Background colors indicate site, from lowest (left) to highest (right) elevation.

Table 1
Ramp rates for thermal tolerance experiments by species. For CT_{min}, species which share a significance letter do not differ significantly with respect to ramp rate ($p < 0.05$). Ramp rates for CTmax experiments did not differ significantly between any species.

Species	CT_{min} ramp rate (mean ± SD °C)	Significance letter (CT_{min} only)	CT_{max} ramp rate (mean ± SD °C)
H. virgulatus	−0.67 ± 0.09	BA	0.74 ± 0.02
H. clypeatus	−0.71 ± 0.08	A	0.73 ± 0.03
H. conjunctus	−0.58 ± 0.01	BC	0.74 ± 0.03
H. hallani	−0.62 ± 0.05	BD	0.76 ± 0.04
H. pugillis	−0.53 ± 0.13	C	0.75 ± 0.05
H. geronimoi	−0.58 ± 0.04	CD	0.76 ± 0.06

Obispo, CA, USA). The entire device was placed into a room regulated at 7 °C. The setup was divided into six lanes, so that each spider could be isolated from the others. Perpendicularly, the lanes were divided into 6 different "zones", from the hot to cold end, so that the initial placement of spiders along the gradient could be randomized.

During the thermal preference trials, the thermal gradient was first turned on and allowed to thermally equilibrate for 30 min. Next, six different spiders were each randomly assigned to one of the six lanes. We then observed spiders and recorded their body temperature every 10 min with a non-contact IR thermometer (Dual Laser IR Thermometer, Model 42511, Exetech Corp, Nashua, NH). At the end of 40 min, we recorded the spiders' final temperatures and concluded the trial. These final temperatures were used in analyses. We compared final temperatures between species using ANOVA and post-hoc Tukey tests. We also calculated T_{pref} range as the middle 50% of temperatures (Angilletta, 2009). Thermal preferences are not static or only associated with one behavior or set of behaviors. Ectotherms can have multiple ranges of preferred body temperatures that they employ to accomplish different physiological tasks and developmental stages (Clissold et al., 2013; Dillon et al., 2009). However, we use this method to achieve baseline information about thermal preference that can be easily compared.

2.6. Thermal performance

2.6.1. Respirometry

We used stop-flow respirometry using a LiCor7000 CO_2 analyzer (Li-Cor Biosciences, Lincoln, NE) and Sable Systems respirometry system (Sable Systems, Las Vegas, NV) to measure rate of CO_2 production ($\dot{V}CO_2$), a proxy for resting metabolic rate. We used a modified repeated measures design, in which we measured each individual at each of seven temperatures, from 10 to 40 °C, at 5 °C intervals (total of 1361 samples, individual sample sizes: *H.* virgulatus = 44, *H. clypeatus* = 58, *H. conjunctus* = 35, *H. hallani* = 42, *H. pugillis* = 51, *H. geronimoi* = 33). See SI for detailed experimental setup. If an individual died between trials, we substituted an individual of the same species and sex for the remainder of the original individual's trials. Therefore, we chose a range of temperatures that fell well below the CT_{max} of the spiders to avoid stress.

We modeled the relationship between $\dot{V}CO_2$ and temperature using the lme function (a linear mixed-effects model) in the R package nlme (Pinheiro et al., 2018). We log-transformed data to improve the normality of residuals. Fixed effects were temperature, species, weight, and the species-by-temperature interaction. Random effects were individual and days since fed. Due to heteroskedasticity in data with respect to temperature, we set a fixed variance structure for temperature, allowing it to increase with increasing temperature (varFixed(~temperature) in nlme). We also calculated mass-scaling exponents using the respirometry package in R (Birk, 2019). Finally, we calculated Q_{10} coefficients, a dimensionless measure of the thermal sensitivity of biological processes. It is calculated as $Q_{10} = (R2/R1)^{10\ °C/(T2-T1)}$, where R1 and R2 are the beginning and ending rates of interest (in this case, mL $\dot{V}CO_2$/hr), and T1 and T2 are the temperatures associated with each rate. The Q_{10} for most processes is around 2, indicating that for each 10 degree increase, the rate doubles (Hochachka, 2002). We calculated Q_{10} values after weight-correcting $\dot{V}CO_2$, as weight was a significant factor in our models.

2.6.2. Locomotion

As jumping is a major means of locomotion for jumping spiders (Chen et al., 2013; Foelix, 2010; Richman and Jackson, 1992), we used a jumping assay to evaluate the effects of temperature on locomotion. We used seven temperatures ranging from 15 to 45° C, at 5 °C intervals (460 total samples, sample sizes: *H.* virgulatus = 11, *H. clypeatus* = 20, *H. conjunctus* = 15, *H. hallani* = 15, *H. pugillis* = 15, *H. geronimoi* = 4). Each spider was run at every temperature if possible. If an individual died between trials, we replaced it with another of the same sex and species for the remainder of the original individual's trials. We shifted the set of temperatures by 5 °C warmer compared to the respirometry experiment to measure locomotor performance closer to the animals' thermal maxima. For each trial, a spider was placed in the incubator at

a given temperature for ten minutes to allow its internal body temperature to equalize with the incubator. We then stimulated spiders to jump by pushing a wooden block toward the spider from behind until it jumped. We attempted to elicit three jumps for each trial. We recorded jumps from above with a GoPro Hero 5 Black set to 240 fps. We used the MTrackJ plugin (Conn, 2012) for ImageJ (Schindelin et al., 2015) to measure jump distance.

For each trial, we averaged the distances for up to three jumps. We then modeled jump distance with the linear mixed effects function lme in the R package lme, with temperature and species as fixed effects and individual as a random effect. We also set a fixed variance structure to allow variance to increase with increasing temperature (varFixed (~temperature) in nlme). Finally, we calculated mass-scaling exponents and Q_{10} values. We calculated Q_{10} coefficients after the response variables were divided by spider weight.

2.6.3. Warming tolerance

Temperatures are predicted to increase in the Santa Rita Mountains by 1.7 –2.8 °C in the next fifty years (Coe et al., 2012). We therefore calculated the buffer between spiders' CT_{max} measures and environmental temperature to predict their ability to cope with future temperature regimes. This is often done with warming tolerance, a metric calculated by subtracting mean annual environmental temperature from the animals' CT_{max} values (Deutsch et al., 2008). We calculated a modified version of this metric by using maximum annual temperatures in calculating warming tolerance to provide the most conservative measure possible. We compared this measure across species using an ANOVA and post-hoc Tukey tests.

2.6.4. Evolutionary history

We generated a pruned phylogenetic tree of SR *Habronattus* species using data from Leduc-Robert & Maddison, 2018 using Mesquite version 3.51 (The Mesquite Project Team, 2018). We tested for phylogenetic signal in elevation (as a continuous variable) and thermal biology data. We used Blomberg's K, implemented using phytools in R (Revell, 2012). For respiration, we calculated Blomberg's K on slopes of the log-transformed linear relationship between $\dot{V}CO_2$ and temperature. For jumping, we calculated K on slopes of the linear relationship between jump distance and temperature. Due to small sample sizes, we used a K value of > 1 to suggest phylogenetic signal within the data (Hebets et al., 2013). As we found no evidence of phylogenetic signal, we did not follow up these analyses with a Phylogenetically-corrected least squares model.

3. Results

3.1. Thermal habitat differences

All four sites differed in their minimum and maximum temperatures (Fig. 1c–d). Both maximum and minimum temperatures differed between all elevational sites (max temperature: $F = 14774$, $p < 0.0001$; min temperature: $F = 10554$, $p < 0.0001$). We found the same pattern with annual breadth (Fig. 1e) ($F = 6656$, $p < 0.0001$). There was no phylogenetic signal in the species distribution along the elevational gradient; closely-related species were not found at more similar elevations than more distantly-related species ($K = 0.789$, $p = 0.3000$).

3.2. Thermal limits

Habronattus geronimoi (the highest-elevation species) had a lower CT_{min} than all other species. Low, middle, and middle-high elevations all had similar CT_{min} values ($F = 12.14$, $p < 0.0001$). *Habronattus clypeatus*, a mid-elevation species, had a higher CT_{max} than the other middle and the middle-high species ($F = 5.6635$, $p = 0.0002$). Relatedness of species had no bearing on their thermal limit values (CT_{min}: $K = 0.789$, $p = 0.0350$; CT_{max}: $K = 0.986$, $p = 0.1390$).

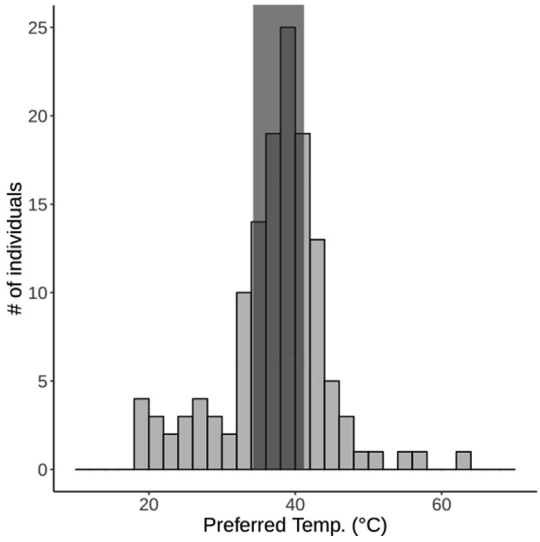

Fig. 3. Thermal preference in Santa Rita *Habronattus*. (a) overall histogram of T_{pref} for all species. There are no differences between species. Dark bar indicates T_{pref} range (temperatures of middle 50% of individuals).

3.3. Thermal preference

All spider species had a mean preferred temperature of 37 °C, and a T_{pref} range of 34.2–41.2 °C (Fig. 3).

3.4. Thermal performance

Spiders produced more CO_2 at higher temperatures, with a Q_{10} of 1.94. Temperature ($F = 637.047$, $p < 0.0001$), species ($F = 4.148$, $p = 0.1001$), weight ($F = 254.712$, $p < 0.0001$), and a temperature by species interaction ($F = 6.390$, $p < 0.0001$) all affected CO_2 production. *H. conjunctus* (a mid-elevation species) produced less CO_2 than the other species, particularly at high temperatures (Fig. 4a). More closely-related species had more similar metabolic rates ($K = 1.34$, $p = 0.0350$). Heavier spiders also produced more CO_2 than lighter spiders, with a mass-scaling exponent of 0.669 averaged across temperatures.

Spiders also jumped farther at higher temperatures, with a Q_{10} of 1.36. Temperature ($F = 141.474$, $p = 0.0130$), weight ($F = 24.75370$, $p < 0.0001$), species ($F = 3.264062$, $p = 0.0071$), the temperature by weight interaction ($F = 16.47918$, $p < 0.0001$), and the weight by species interaction ($F = 2.86450$, $p = 0.0150$) all affected jump distance. *H. hallani* jumped significantly farther than *H. clypeatus* ($p = 0.0032$). *H. hallani* also jumped significantly farther than *H. geronimoi* ($p = 0.0030$) (Fig. 4b). There was no phylogenetic signal in these results ($K = 0.591$, $p = 0.5970$). Heavier spiders also jumped farther than lighter spiders, with a mass-scaling exponent of 0.23 averaged across temperatures.

3.5. Warming tolerance

All species showed high warming tolerance, broadly recapitulating the species differences in CT_{min} ($F = 46.77$, $p < 0.0001$. *H. geronimoi* had the highest warming tolerance, followed by *H. pugillis* (Fig. 5). There was more variation among the middle and low elevation species. *H. clypeatus* had a higher warming tolerance than both *H. conjunctus* and *H. hallani.* Relatedness was not a factor in these results ($K = 0.035$, $p = 0.3860$).

4. Discussion

Our data suggest that cold tolerances are more variable across

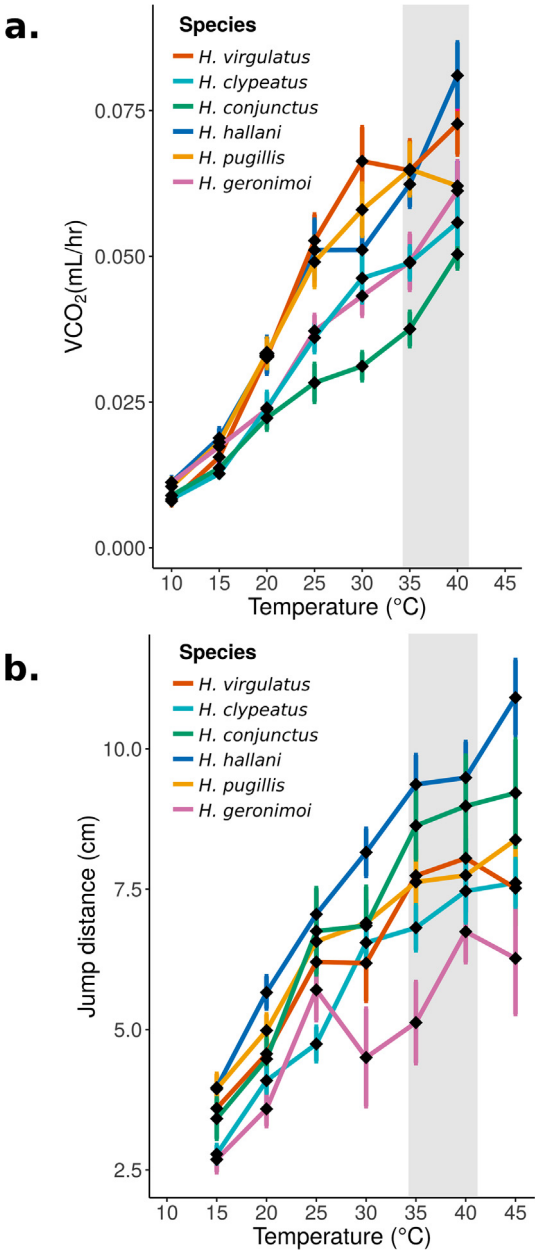

Fig. 4. Thermal performance in Santa Rita *Habronattus*. (a) carbon dioxide emission of SR *Habronattus* across seven different temperatures. *H. conjunctus* has significantly lower carbon dioxide emission than the other six species. Grey bar indicates the T_{pref} range (middle 50% of individuals) (b) jump distance in SR *Habronattus* species across seven different temperatures. No differences are seen between species when body size is taken into account. Grey bar indicates the T_{pref} range (middle 50% of individuals).

elevation than heat tolerances, a pattern commonly known as Brett's rule (Polato et al., 2018). We also found interactions between thermal performance and thermal preference, suggesting that thermal biology in SR *Habronattus* represents a complex interplay between physiology and behavior. Finally, we find support for high warming tolerance and species resilience in SR *Habronattus* to global climate change.

4.1. Evidence for Brett's rule

Of all the thermal variables measured, CT_{min} was the only one that showed clear differences between elevational sites. We found the lowest CT_{min} in the highest-elevation species, *H. geronimoi* (Fig. 2b), corresponding with the lower minimum temperatures in high elevation

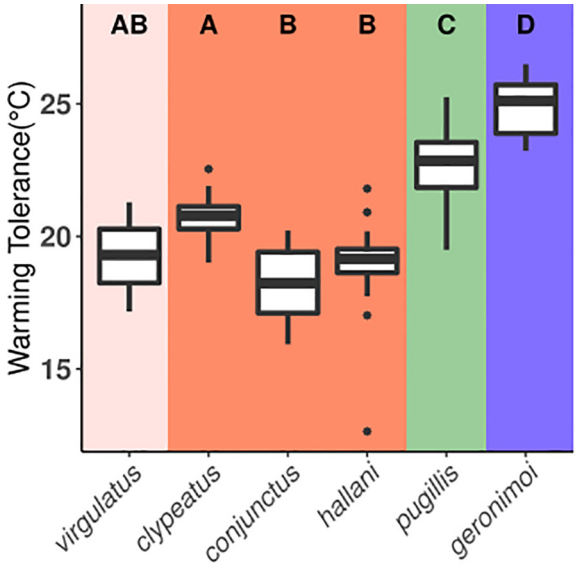

Fig. 5. Warming tolerance for Santa Rita *Habronattus* species. Warming tolerance calculated by CT_{max} – max temp of warmest month. Background colors indicate site, from lowest (left) to highest (right) elevation.

habitats. However, this was not recapitulated with a similarly low CT_{max} in this species (Fig. 2a). In fact, we found that all SR *Habronattus* species had high CT_{max} measurements that were conserved across the elevational gradient. CT_{max} values ranged from 52 to 55 °C on average. These values are likely comparable to the CT_{max} of 51–52 °C found for desert-dwelling spiders (Franken et al., 2018; van den Berg et al., 2015), which were measured under a slower ramping rate, and higher than species found in the Namib, assessed using a non-ramping method (Lubin and Henschel, 1990).

This pattern of invariant heat tolerance and variable cold tolerance supports Brett's rule (Nowrouzi et al., 2018; Polato et al., 2018; Slatyer et al., 2016; Slatyer and Schoville, 2016). Recent work has suggested that Brett's rule applies most strongly in tropical habitats with low thermal variability (Polato et al., 2018). Our study provides support for Brett's rule in desert habitats that have high thermal variability and suggests that this rule may be more universal than previous considered.

The mechanisms behind Brett's rule fall broadly into three non-exclusive categories (Sunday et al., 2019). First, there may be elevationally invariant selection on CT_{max}. That is, either all elevations are exposed to similarly hot temperatures at some point during the year (Pincebourde and Casas, 2019; Sunday et al., 2014), or animals behaviorally thermoregulate such that they do not experience their thermal maxima (Huey et al., 2003; Muñoz et al., 2016). Second, in recent range expansions, there may be a lag between distribution shifts and concordant changes in CT_{max} (Lancaster, 2016). There also may be genetic or physiological constraints preventing CT_{max} from reaching habitat-appropriate values (Araújo et al., 2013). It is possible that any (or all) of these hypotheses could be in play for SR *Habronattus*. With respect to elevationally invariant selection, we know that SR *Habronattus* have strong thermal preferences that do not vary between species (Fig. 3.). If spiders are able to thermoregulate within their preferred ranges, this could potentially relax selection on CT_{max} and produce the observed patterns. With respect to biogeographical history, it is hypothesized that the Santa Rita mountain range was part of a glacial refugium, suggesting that SR *Habronattus* diversified and dispersed to their current ranges sometime between 30 kya and 2 mya (Leduc-Robert and Maddison, 2018; Masta, 2000). Given this relatively short time frame, it is possible that there has been insufficient time for CT_{max} to evolve. Finally, it is unclear whether genetic or physiological constraints may be impacting CT_{max} in SR *Habronattus*. Studies examining the genetic basis of thermal tolerance across *Habronattus* could evaluate whether

there is support for this hypothesis.

Despite the lack of elevational signal in CT_{max} measurements, some interesting patterns in thermal limits can be seen at intermediate elevations. For example, *H. clypeatus* had a higher CT_{max} than the other middle and middle-high species but was indistinguishable from either the low or high species (Fig. 2a–b). Because we find differences in CT_{max} between species found at the same middle elevation site, this site may be more thermally diverse. The measured thermal limits of some species fit well with what we know about their ecology. For example, *H. hallani* had a low CT_{max} and has been shown to exhibit swimming behavior (rare in salticids), and suggests specialization for a cooler microhabitat (Stratton et al., 2004). This suggests that our measured thermal limits may reflect differences in thermal microhabitats

4.2. Integration of behavior and physiology

It is striking that despite a large thermal breadth in SR *Habronattus* (~40 °C), the thermal preference (T_{pref}) range only encompasses about 7 °C and does not vary between species (Fig. 3). The T_{pref} range of SR *Habronattus* was higher than most spiders (particularly fossorial species) but fell within the range of wolf spiders found in the Alps (Frick et al., 2007). Having narrow thermal preference is one way that animals may behaviorally buffer against environmental extremes. If spiders consistently seek out microhabitats within a narrow range of temperatures, there is less risk of exposure to temperatures exceeding their CT_{max}. This assumes that microhabitats that are within the preferred temperature range are consistently available and requires future study to assess the thermal heterogeneity of relevant microhabitats. It may also be more difficult to buffer against CT_{min}, given that environmental heterogeneity tends to be decreased at night, when minimum temperatures occur (Ghalambor et al., 2006; Muñoz et al., 2016). SR *Habronattus* seem more limited by cold tolerance rather than by heat, especially given that their habitats attain temperatures well below their CT_{min} (Fig. 1c). This could pose a substantial challenge to their thermoregulatory ability.

Interestingly, the T_{pref} range sits among the warmest temperatures that we measured in performance trials (Fig. 4). At those temperatures, jumping ability either continues to increase or plateaus, suggesting spiders in the T_{pref} range are approaching the T_{opt} for locomotor activity. In contrast, metabolic rate increases steadily throughout this range, supported by a higher Q_{10} value for metabolic rate compared to jumping (Q_{10} of 1.9 vs. 1.4). This suggests that maintenance costs rise faster than performance ability, perhaps indicating that a decline in aerobic scope may constrain performance at high temperatures in or above the T_{pref} range (Pörtner, 2001, 2010). We have also found previously that *H. clypeatus* courtship signals plateau around 40 °C (Brandt et al., 2018). Taken together, this suggests that spiders may choose temperatures at which courtship performance is optimized.

We found few differences between species with respect to thermal performance, and none that appear to relate to elevation. Again, this could be related to either invariant selection or constraints. There is some evidence that metabolic rates are phylogenetically constrained. *H. conjunctus* had a lower respiration rate and was less temperature-sensitive with respect to metabolic rate (Fig. 3a). *H. conjunctus* is the most distantly-related of all SR *Habronattus* species (Fig. 1b). (Leduc-Robert and Maddison, 2018). With respect to locomotion, the only differences between species are between the two smallest by mass and the largest, with no effect of relatedness.

4.3. Implications for future species distribution patterns under climate change

SR *Habronattus* show large thermal breadths and warming tolerances (Fig. 2,5). One goal of this study was to bring these data to bear on the question of resilience in *Habronattus* given changing global climate and the massive worldwide declines in arthropod populations (Hallmann et al., 2017; Lister and Garcia, 2018). SR *Habronattus'* large warming tolerances may represent a substantial buffer against future increases in habitat temperature (Fig. 4). The predicted increase of 1.7–2.8 °C should make little difference to SR *Habronattus*, with a warming tolerance of > 20 °C for each species (Fig. 5). This suggests that these species are relatively robust to future thermal shifts.

We suggest that SR *Habronattus* will be resilient to change, despite the following important caveats: First, there are known drawbacks to using WorldClim2 temperature data (discussed for eg. by Faye et al., 2014; Potter, Woods, & Pincebourde, 2013). Principally among these is the fact that interpolated weather station data are collected at temporal and spatial resolutions which bear little relevance to conditions experienced by small animals living on the ground, meaning that these average environmental temperatures do not reflect the daily extremes that may be driving selection (Sunday et al., 2019). Because of these limitations, warming tolerances calculated based on climate temperatures are likely to overestimate resilience to climate change compared to predictions made based on microclimate data (Pincebourde and Casas, 2019; Sunday et al., 2019). Second, opportunities for behavioral thermoregulation may differ between habitats leading to species-specific decoupling of body and air temperatures. For instance, *H. virgulatus,* which experiences mostly open rocky habitat may behaviorally thermoregulate differently from *H. geronimoi*, which lives on pine duff. Future work is underway to understand SR *Habronattus'* use of thermal microhabitats and behavioral thermoregulation on scales relevant to the animals. Finally, acclimatization or ontogenetic shifts in thermal tolerances are likely to alter CT_{max} and correspondingly, the estimates of warming tolerance (Bowler and Terblanche, 2008; Levy et al., 2015; Pincebourde and Casas, 2016). Future work will address the effects of life stage and season on thermal tolerance. With these caveats in mind, it is likely that our methods have at least somewhat overestimated the robustness of SR *Habronattus* to temperature increases due to climate change. However, we show such large warming tolerances, that a predicted overestimation of 7–10 °C as suggested by Pincebourde 2019 would still give SR *Habronattus* species a comfortable thermal tolerance buffer in the face of climate change. It should also be noted, however, that thermal stress can disrupt animals in ways that cannot be measured with physiological assays. In at least one species of SR *Habronattus,* courtship and mating are affected by temperature (Brandt et al., 2018). Finally, there is evidence of widespread historic introgression across the group (Leduc-Robert and Maddison, 2018). If changing climate puts allopatric *Habronattus* species into contact, complex dynamics involving temperature-dependent courtship signals, mate preference, and physiological tolerances may come into play.

5. Conclusions

By studying multiple measures of thermal biology and behavior, we provide support for Brett's rule along a desert elevational gradient, suggesting that extreme low temperatures are an important selective agent in determining species distributions. Specifically, we found that only cold tolerance, and no other thermal biology metrics, had explanatory power regarding species distribution patterns in SR *Habronattus*. This lends weight to the hypothesis that Brett's rule applies broadly across latitudinal (Addo-Bediako et al., 2000; Ghalambor et al., 2006; Kimura, 2004) and elevational clines. We also found that SR *Habronattus* had high CT_{max} measurements and little variation between species. The lack of variation may reflect (1) geographically invariant selection on responses to hot temperatures, (2) genetic constraints on the evolution of these traits and/or (3) the importance of behavioral thermoregulation. Given that temperature preferences are conserved between species, we suggest that behavioral plasticity might be important in allowing these physiologically-similar species to live in very different microhabitats. Finally, SR *Habronattus* have high warming tolerances, suggesting that these species should be robust to future increases in habitat temperature. Ongoing work will build upon these

results by examining variation in spider habitats at scales relevant to the animals, and further integrating how behavior interacts with their thermal biology. Additionally, studies comparing different species assemblages across the landscape can be leveraged to test hypotheses about how thermal tolerance differences have arisen (e.g.: local adaptation, environmental filtering).

CRediT authorship contribution statement

Erin E. Brandt: Conceptualization, Methodology, Investigation, Software, Data curation, Visualization, Writing - original draft, Writing - review & editing, Funding acquisition. **Kevin T. Roberts:** Conceptualization, Methodology, Writing - review & editing. **Caroline M. Williams:** Conceptualization, Methodology, Writing - review & editing, Resources, Funding acquisition, Supervision. **Damian O. Elias:** Conceptualization, Writing - review & editing, Funding acquisition, Supervision.

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Data accessibility

Data are available from Dryad at doi: https://doi.org/10.6078/D1X98S.

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